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POLLINATION AND CROSS-FERTILIZATION
IN THE JUAR PLANT (*ANDROPOGON*
SORGHUM, BROT)

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BY

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INTRODUCTION.

THE work of classifying the varieties of *juar* grown in the Central Provinces and Berar has been in progress during the past six years. At an early stage in the enquiry evidence of natural cross-pollination was observed. It was, therefore, necessary to discover to what extent the process takes place in this crop, as not only would its occurrence account for the origin of many of the varieties, but would also militate against the successful introduction of improved varieties. The material on which the enquiry was started was the collection of *juars* from all districts in the Central Provinces and Berar sent in to the Central Provinces and Berar Exhibition of 1908.

The usual method of single plant culture was employed in order to study the characters of the plant as a preliminary to the work of classification. In the first year of cultures, evidence of natural cross-pollination was discovered. Up to the present nothing has been published in India regarding the pollination of this crop. It is proposed in the following note to give an account of the process as observed on the Nagpur Farm.

THE INFLORESCENCE.

The inflorescence in *Andropogon Sorghum* consists of a loose or congested, erect or recurved (goose-necked) panicle. On the branches of the panicle the

spikelets are arranged in pairs, a sessile hermaphrodite spikelet and a pedicelled neuter. At the apex of the branches there are three spikelets, a sessile hermaphrodite spikelet accompanied by two pedicelled neuters. These neuters represent reduced male flowers and it is the custom to describe them as male spikelets. In rare cases the male flowers are functional (Fig. 1), but for the purpose of this note they are described with regard to their usual condition and in accordance with the description in the "Flora of British India."¹

The flowers under observation opened in a fairly regular order. The terminal hermaphrodite spikelet of the branch opened first and was followed by succeeding flowers on the branch until 3 or 4 had opened. At the same time the flowers on the adjacent and next lower branches were opening in the same order, so that we thus have the flowers near the end of the upper branches opening together during the same flowering period. On the second night when flowering recommenced the lower flowers on the upper branches opened, along with the terminal flowers on branches lower down. Flowering proceeded in this manner until all the flowers had opened. Except during the flowering period on the first night it is extremely difficult to follow the order of the opening of the flowers, as two-thirds of the panicles may be covered with flowers.

POLLINATION.

From the apex of the opening glumes the first essential part to appear was the tip of the stigmas. This was seen in some cases at least 24 hours before the glumes fully opened. At various hours during the night the glumes opened fully. During the months of March and April, the larger number of flowers opened between the hours of 1 A.M. and 4 A.M., but stray flowers opened as early as 11 P.M. In June and July the flowers opened mainly between 3-30 A.M. and 4-30 A.M., but on rainy nights occasional flowers opened as early as 8-30 P.M., and this continued till 4 P.M., the following afternoon.

The following tables give the numbers of flowers observed to be open. Table I records the number of flowers in 16 panicles on six successive nights from the 24th March, 1914, the total number of flowers at each period on successive nights being added together. Table II similarly records the number of flowers in 6 panicles for six successive nights from the 19th August, 1915.

¹ Hooker, J. D. *Flora of British India*, vol. VII, p. 183.



Fig. 1.
Male Pedicelled spikelet of
A. Sorghum \times 5.
The pores in the anthers
are well seen.



Fig. 3.
Hermaphrodite sessile spikelet of
A. Sorghum \times 5.
The anthers have dehisced without the
stamens falling out.



Fig. 2.
Hermaphrodite sessile spikelet of *A. Sorghum* \times 5.
Glumes closed with stigmas outside and still fresh.
Photograph taken at 4 P. M.

TABLE I.—(March 24—29, 1914.)

TABLE II.—(August 19—24, 1915.)

Hour	No. of flowers at each period for six nights	Hour	No. of flowers at each period for six nights
From 11 P. M. to midnight.	358	From 7.30 P. M. to 8.30 P. M.	16
" midnight to 1 A. M.	1,096	" 8.30 P. M. " 9.30 P. M.	80
" 1 A. M. " 2 A. M.	1,267	" 9.30 P. M. " 10.30 P. M.	99
" 2 A. M. " 3 A. M.	1,233	" 10.30 P. M. " 3 A. M.	154
" 3 A. M. " 4 A. M.	1,093	" 3 A. M. " 2.30 A. M.	483
" 4 A. M. " 5 A. M.	797	" 3.30 A. M. " 4 A. M.	687
" 5 A. M. " 6 A. M.	521	" 4 A. M. " 4.30 A. M.	320
" 6 A. M. " 7 A. M.	443	" 4.30 A. M. " 7.30 A. M.	81
" 7 A. M. " 8 A. M.	439	" 7.30 A. M. " 4 P. M.	96
" 8 A. M. " 9 A. M.	214		
" 9 A. M. " 10 A. M.	117		
" 10 A. M. " 11 A. M.	46		

Ball¹ simply mentions that the flowers open in the morning without specifying the hour. The above observations differ from those of Koernicke² who finds the flowering to be at its height between 8 A. M. and 9 A. M., and states further that it may continue throughout the day. It is clear from the tables above that only occasional flowers open during the day. The latest instance of an open flower was 4 P. M. on a rainy day. The inference naturally is that the opening of the flowers is influenced by the moisture conditions of the air.

As the glumes began to open with the swelling of the lodicules, the stigmas which had been protruding slightly were seen surrounded by the three anthers. Elongation took place gradually, the tip of the stigmas still remaining above the anthers. Finally the rate of elongation of the stamens increased, the lateral stamens usually lengthening first until they surpassed the stigmas. As the pressure between the glumes was relieved by the opening of the glume and the exertion of the anthers, the anthers became more distant from each other and the lower hairs on the stigmas could be seen spreading out. The two lateral stamens finally elongated rapidly and their weight caused them to fall out. With the resulting relief of pressure the stigmas, which, up to the present, had been in the antero-posterior plane, moved into the lateral plane of the flower and rapidly expanded into the space left between the outer glumes. The posterior stamen then fell out. The dehiscence of the anthers took place at various times. Generally the lateral pores were visible just as the glumes opened, but in a considerable number of cases dehiscence took place only after the anthers

¹ Ball, C. R. *Am. Br. Mag.* 1910, p. 283.

² Koernicke, F. *Handbuch des Getreidebaues.*

were pendent. In a small number of flowers in the more compact type of panicle the anthers did not assume the pendent position remaining partially within the glumes close to the stigmas (Fig. 3) : while in a few of the last flowers to open for the flowering period of that night there was no dehiscence of the pendent anther. The opening of the pores of the anthers caused no scattering of pollen and it was only when the anthers had fallen over that pollen escaped. The flowers therefore are protogynous as is also admitted by Koernicke¹ and Kirchner.² The details of the process related above vary considerably, however, from those described by the two authors.

The whole process from the time of the opening of the glumes till the anthers assumed the pendent position occupied 10 minutes. Instances were not wanting in which the process took place in as short a time as 3 minutes, while, on the contrary, the process may occupy 30 minutes. Finally as stated above the stamens may never become pendent.

The flowers of the *juar* opened only once, the glumes remaining open for 2—3 hours, the closing of the glumes being a much more gradual process than the opening. The stigmas remained outside after the glumes had closed and appeared quite fresh for as long a period as 24 hours after the glumes had closed. (Fig. 2.) The length of time taken for the whole panicle to complete flowering varied with the size of the inflorescence and the number of flowers. The average time was about seven days.

From the observations it is evident that cross-pollination between flowers of the same panicle is the rule, the pollen from the higher and earlier opening flowers falling on and pollinating the stigmas of lower and later flowers. This is the conclusion also arrived at by Fruwirth³. Cross-pollination by foreign pollen can only take place in the first flowers to open, and possibly in the case of late opening flowers whose anthers do not dehisce. Self-pollination can only take place in late opening flowers whose stigmas remain surrounded by the anthers which do not fall out, but even in those cases the chances are in favour of pollination from higher flowers in the same inflorescence. Though typically anemophilous the flowers of the *juar* were visited in considerable numbers by insects. In addition to small beetles which crawled over the panicle, the flowers were regularly visited by bees. During the months of March and April the first bee to arrive soon after day-light was a small bee with white stripes (*Apis florea*). This was followed by the large wild bee

¹ Koernicke, F. *Loc. cit.*

² Kirchner, D. *Neue Beobachtungen*, p. 11.

³ Fruwirth, C. *Die Züchtung der landwirtschaftlichen Kulturpflanzen*, Bd. V, 1912, p. 59.

(*A. dorsata*) and another small bee with yellow stripes (*A. indica*?). The bees worked carefully over the panicles, picking out the recently opened flowers from whose anthers they milked the pollen with their first pair of legs. By 8 A.M., the visits of the bees had ceased. Undoubtedly the bees are an important agency in bringing about pollination by foreign pollen.

FREQUENCY OF FOREIGN POLLINATION.

Foreign pollination is much more common in some varieties than in others and observations show that it is less frequent in the compact types of inflorescence and more frequent in the looser types. Amongst the latter foreign pollination is more common in the types with short glumes than in those with long glumes. These observations are in accordance with expectation, the flowers in the compact type of inflorescence being close together and as pointed out above the anthers, in some cases, never falling out of the glumes, while in the flowers with long glumes these furnish a certain amount of protection.

Taking as a basis for comparison the occurrence of foreign pollination in the single plant cultures the following table shows the relative frequency :—

TABLE III.

Year	COMPACT TYPES			LAX TYPES WITH SHORT GLUMES			LAX TYPES WITH LONG GLUMES		
	No. of heads sown	No. of crossed flowers	No. of crossed flowers per 100 heads	No. of heads sown	No. of crossed flowers	No. of crossed flowers per 100 heads	No. of heads sown	No. of crossed flowers	No. of crossed flowers per 100 heads
1909	25	3	12
1910	40	6	15
1911	17	4	24	46	24	52	30	8	27
1912	29	6	20	77	223	289	2	3	13
1913	87	198	227	26	9	34
1914	196	413	209
1915	107	126	114

The highest number of crossed flowers was found in Tharthur which showed 165 in 18 lines or 817 crossed flowers per 100 heads.

The percentage of crossing obtained by counting a given number of plants and noting those which were untrue to type is 6% or 97 plants out of 1,577 in a loose type of panicle with short glumes, and only 6% or 2 plants out of 292

in a compact type of panicle. Tharthur taken in the same way gave 20% or 165 plants out of 828. Ball¹ puts the highest number at 50%.

EXAMINATION OF CROSSES.

Grain characters. The colour of the grain is either red, white, or yellow. The red grains owe their colour to the presence of a red coloured cell sap in the cells of the pericarp. This colouring extends also to other parts of the plant, particularly to the leaves. During the vegetative period the red colour is masked by the chlorophyll, but when the plants ripened the leaves of the red grained plants stand out on account of the red colouring matter contained in the leaves. The yellow colour is similarly due to a yellow coloured cell sap in the cells of the pericarp. The colour likewise extends to the foliage of the plant but at the time of ripening is less noticeable, the darker yellow leaves of the yellow grained plants being liable to be overlooked by a casual observer. The leaves of the white grained plants at harvest are straw coloured. The colour of the plant can be detected at the time of flowering, the stamens and stigmas of the red grained plants being orange, and those of the yellow and white pale yellow.

CROSS I.²

In the first natural cross observed, namely, Lal Juar, 1908, the head sent in may be taken for our purpose as an F_1 plant, heterozygous with regard to the colour of the grain containing a simple pair of allelomorphs, presence and absence of red. The number of plants was unfortunately small, but the numbers indicated that this cross conformed to the Mendelian interpretation.

CROSS II.

In the same year Shenaliwani D proved to be a heterozygous plant for the same pair of characters.

CROSS III.

In 1910 Lal Guranj, which had been true to the red character of the grain in the single plant cultures, began to split into red and white. This was evidently a case of natural cross-pollination in the single plant cultures, the hybrid being heterozygous for the same pair of allelomorphs.

¹ Ball, C. B. *Loc. cit.*, p. 283.

² The crosses dealt with in this paper were left unprotected. The reasons for doing so were : first, that the majority of the observations were confined to crosses in the compact type of panicle and the lax type with long glumes in both of which the percentage of natural cross-pollination is extremely low ; and second, that the characters under consideration are well marked and the small amount of crossing which occurred was immediately detected.

CROSS IV.

Amongst five red grained *juars* from Gunji, secured in the harvest of 1909, three were found to be heterozygous for red and white in the line cultures of 1910, giving numbers closely corresponding to the Mendelian expectation. Further line cultures in 1911 again gave fairly approximate results. The following table sets out the combined figures obtained from these four natural crosses which occurred amongst varieties having a compact type of inflorescence:—

TABLE IV.

1908	2 plants red		
				Red		White
1909	25		8
Ratio	3 1		1
1909 Plants used as parents				4 21		8
				Red	Red	White White
1910	All	239	87 All
Ratio	2·7		1
1910 Plants used as parents				12 25		14
				Red	Red	White White
1911	All	926	261 All
Ratio	3·5		1
1911 Plants used as parents				3 11		5
				Red	Red	White White
1912	All	118	70 All
Ratio	1·7		1

CROSS V.

From 1910-1913 Thaithur, which had been a pure white for the two previous years, produced a small number of red grained plants in the single plant cultures. This was unexpected and the explanation lay in one of two directions:—Either these reds were rogues, *i.e.*, plants from stray seeds, or they were crosses. The small number of red plants might support either supposition. On resowing they proved to be crosses.

CROSS VI.

Nilwa in 1910 produced in the line culture seven red grained plants, the rest of the line being white grained. On resowing, these red grained plants proved to be crosses splitting into red and white. Nilwa appears to be a variety very liable to cross-pollination, the percentage of crosses being as high as 6%.

The following table sets out the combined figures obtained from the last two natural crosses which occurred in varieties having a loose type of panicle with short glumes:—

TABLE V.

1910	7 plants red			
				Red		White	
1911	331		146	
Ratio	2.2		1	
1911 Plants used as parents				2	30	3	
				Red	Red	White	White
1912	All	647	309	All
Ratio	2.1		1	
1912 Plants used as parents				5	25	9	
				Red	Red	White	White
1913	All	816	475	All
Ratio	1.8		1	

CROSS VII.

Four of the red grained plants from Gunji in 1910 were found to be heterozygous for red and yellow in the line cultures of 1911. The numbers correspond with those expected under Mendel's law. Further line cultures in 1912 gave again an almost mathematical demonstration of Mendel's law.

TABLE VI.

Gunji Red.

1911	4 plants red			
			Red		Yellow	
1912	94		32	
Ratio	2.9		1	
1912 Plants used as parents			<div><div>3</div><div>10</div><div>7</div></div>			
			Red	Red	Yellow	Yellow
1913	All	300	102	All
Ratio		2.9	1	

CROSS VIII.

One of two yellow grained *juars* from Gunji secured in the harvest of 1909 was found to be heterozygous for yellow and white grain in the cultures of 1910. On further culture the same phenomenon was observed. The number indicated segregation as described by Mendel.

TABLE VII.

Gunji Yellow.

1909	...	1 plant yellow			
		Yellow			White
1910	...	12			4
Ratio	...	3			1
1910 Plants used as parents.		<div style="display: flex; justify-content: space-around; align-items: center;"> 4 5 </div>			4
		Yellow	Yellow	White	White
1911	...	All	135	27	All
Ratio	...		5	1	

Thirty yellow grained plants of Gunji from the harvest of 1912 were grown and the result in 1913 was in accordance with the above observation. In seven cases evidence of further natural crossing was apparent but this does not vitiate the result appreciably.

TABLE VIII.

Gunji Yellow.

1912	..	30 plants yellow					
		17	6		7		
1912 Plants used as parents		Yellow	Yellow	White	Yellow	White	Red
1913	..	All	114	28	165	51	10
Ratio	...		4	1	3.2	1	

CROSS IX.

The next cross Gunji resulted in the production of three types of plants distinguished as Red grained, Yellow grained, and White grained, respectively. Taking the families in which all three colours occur we find the total Red, 340, Yellow, 96, and White, 139. This approximates to a 9 : 3 : 4 ratio fairly closely, the expectation on that supposition being Red, 325 ; Yellow, 105 ; White, 140. The red grained plants proved in further cultures to be of three types, the yellow of two and the white of one type. On crossing a number of the whites with one of the pure yellows, however, the whites proved to be of at least two kinds, namely, those which gave a red grained F_1 plant and those which gave a yellow grained F_1 plant.* This leads to the assumption that some of the whites are really undeveloped reds and only require the addition of yellow to cause the red colour to develop. The complementary factors that compose the red colour are separate, one being contained in the white grained plant and the other in the yellow grained. When both of these combine the red colour is produced. The simplest solution suggested by Mr. H. Martin Leake to whom I desire to tender my thanks for the suggestion is one involving only two factors R (red) and Y (yellow). The simplest case of such a combination is one in which $RrYy$ will give 12 Red, 3 Yellow, 1 White, supposing red completely masks yellow. If we suppose that Red can only develop in the presence of yellow then $RrYy$ gives 9 Red, 3 Yellow, 4 White.

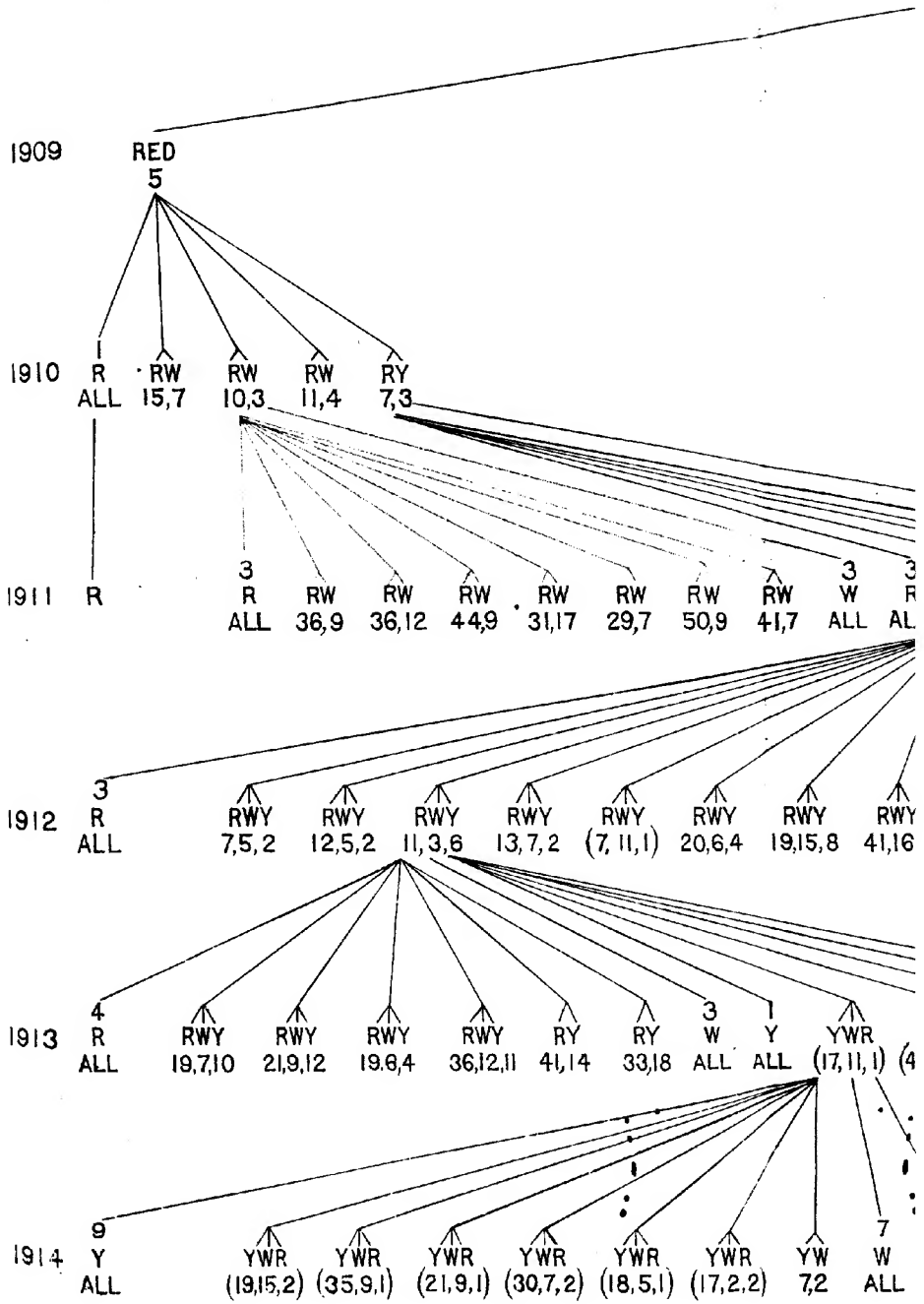
The actual numbers are given in the table on page 212.

* *Artificial cross-pollination.* Juar presents few difficulties with regard to artificial cross-pollination. The inflorescence can be mutilated very considerably without apparently interfering with the fruit development of the remaining flowers. The fruits also develop freely inside protecting envelopes. The method employed was to select a plant in which the panicle was just emerging from the leaf sheath. In the afternoon all the topmost branches, with the exception of three, were removed; at the same time the lower branches were removed to expose the rachis which forms a useful support on which to fasten the protecting envelope. The removal of the lower branches further prevented the chance of pollen from the lower flowers adhering to the mouth of the envelope during subsequent examination of the protected flowers. All the flowers were removed from the three top-most branches except one near the tip of each branch and one near the lower end of the branch. The glumes were thereafter gently forced apart by holding the awn with forceps and pressing the glumes laterally. The flower was thus easily castrated and was then protected in the usual way by an envelope. When the stigmas were mature—this being ascertained by removing the envelope, when, if the stigmas are mature, the glumes are found to be open with the stigmas extruding—pollen was applied. It is necessary to make the examination early in the morning, though castrated flowers in envelopes remain open for a longer time than exposed flowers. After the grain had set the bottom of the envelope was torn off, the remaining portion serving the double purpose of a distinguishing mark and a protection from birds. Control flowers showed that there was little danger of accidental self-pollination during the process of castration if ordinary precautions were taken.

TABLE IX.
Gungi Red.

1908		1 plant red											
					Red		Yellow.									
					5(a)		2(b)									
					9		6									
		RRYY 1(a)		RRYY 1(a)		RRYY 3(a)		rrYY 1(b)		rrYY 1(b)		rrYY 1(b)				
		Red		Yellow		Red		White		Yellow		White				
		All		7(c)		3(d)		36		All		12				
		All		9		3		42		All		12				
		3(c)		3(c)		3(c)		4rYY 1(c)		3(g)		3(g)				
		Red		Red		Yellow		Red		Yellow		White				
		All		94		24		24(e)		5(f)		7(g)				
		All		72		24		24		8		9				
		3(e)		4(e)		4(e)		9(e)		4(f)		1(f)				
		Red		White		Red		Yellow		White		White				
		All		93		22		94		32		6				
		All		66		22		96		32		6				
		4(h)		2(h)		4(h)		1(i)		3(i)		2(i)				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
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		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41		45				
		All		96		32		125		56		45				
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		All		96		32		125		56		45				
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		All		74		32		125		41		45				
		All		96		32		125		56		45				
		Red		Yellow		Red		Yellow		White		White				
		All		74		32		125		41						

1908



The accompanying diagram shows the relationships between the line cultures of each year. It will be noticed that there are numerous natural crosses. These numbers have been enclosed in brackets. The figures below each letter give the number of plants of the colour occurring in the line.

Glume characters. The varieties of *juar* can be divided into two main groups as regards the length of the glumes in comparison with the size of the grain. The commoner type has the glumes shorter than the grain which is thus exposed and appears to be held in a cup formed by the glumes; the less common type has the glumes much longer than the grain. The glumes meet above and conceal the grain. The long glume character is, so far as observation goes, always associated with a loose type of panicle.

Cross X.

The first cross between the long glumed *juar* and the short was noticed in 1911 when in a pure line of Galgalya six short glumed heads were observed. These on further culture split into long and short in a ratio which corresponds very closely with the Mendelian ratio, 3 : 1.

TABLE X.

Galgalya (long glume).

1911	6 plants short			
				Short			Long
1912	60			20
Ratio	3			1
1912 Plants used as parents	...			<div style="display: flex; justify-content: space-around; align-items: center;"> 4 7 </div>			3
				Short	Short	Long	Long
1913	All	192	61	All
Ratio		3.1	1	

CROSS XI.

In 1911 amongst the white grained plants of Cross No. V, two lines were found containing plants with long and short glumes respectively, the proportion of which was very nearly 3 short : 1 long. It was therefore obvious that the parent heads from which those lines were sown were heterozygous for the long and short glume characters respectively.

TABLE XI.

Nilua (short glume).

1910	2 plants short					
			Short			Long		
1911	32			18		
Ratio	1·7			1		
1911 Plants used as parents			14		17		16	2
			Short	Short	Long	Long	Short	Long
1912	All	271	87	All	42	6
Ratio		3·1	1			
1912 Plants used as parents			16		65		9	
			Short	Short	Long	Long		
1913	All	1236	422	All		
Ratio		2·9	1			

CROSS XII.

In 1911 a short red *juar* was observed in the pure line of white Galgalya. This on resowing split into four types of heads—red short, red long, white short, and white long. The original short red was therefore heterozygous for two pairs of allelomorphs, viz., red and white in the colour of the grain, and shortness and longness in the length of the glume.

TABLE XII.
Galgalaya (red short glume).

1911		1 plant red short																			
				Red Short								Red Long				White Short				White Long			

SUMMARY.

Andropogon Sorghum, Brot. is protogynous. Normally the flowers are pollinated from the higher flowers of the same panicle. The flowers though typically anemophilous are regularly visited at certain seasons by insects, chiefly bees. This undoubtedly leads to natural cross-pollination, the liability to which depends on the structure of the panicle, being greater in the laxer forms.

Flowering takes place in a fairly regular order. During the months over which the observations extended, the majority of the flowers opened between 2 and 4 A.M. Stray flowers may open before or after, this being influenced by the moisture conditions of the air.

In the grain the red colour and the yellow colour behave as simple allelomorphs, as also do the red colour and the white colour, red being in both cases dominant. Likewise the yellow colour and the white colour may behave as simple allelomorphs, or the heterozygote may be red, behaving as a dihybrid with a 9 : 3 : 4 ratio for red, yellow and white, respectively. The simplest explanation is that certain white grained plants are undeveloped reds requiring the presence of yellow to cause the red colour to develop.

In the glumes the long character and the short character behave as simple allelomorphs.

NAGPUR,

October 1915.

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